

# Physiological and ecological significance of sunflecks for dipterocarp seedlings

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## Abstract

Irradiance is highly dynamic in many plant canopies. Photosynthesis during sunflecks provides 10–90% of daily carbon gain. The survivorship of tree seedlings in the deeply shaded understorey of tropical rain forests is limited by their ability to maintain a positive carbon balance. Dipterocarp seedlings from the SE Asian rain forest were used as a model system to test novel aspects of the physiological and ecological significance of sunflecks. First, understorey seedlings experienced leaf temperatures up to 38 °C in association with sunflecks. Under controlled environment conditions, the inhibition of carbon gain at 38 °C, compared with 28 °C, was significantly greater during a sequence of sunflecks (–59%), than under uniform irradiance (–40%), providing the same total photosynthetic photon flux density (PPFD). Second, the relative enhancement effects of elevated [CO<sub>2</sub>] were greater under sunflecks (growth +60%, carbon gain +89%), compared with uniform irradiance (growth +25%, carbon gain +59%), supplying the same daily PPFD. Third, seedling growth rates in the forest understorey were 4-fold greater under a dynamic irradiance treatment characterized by long flecks, compared with a regime of short flecks. Therefore, stresses associated with dynamic irradiance may constrain photosynthetic carbon gain. Additionally, seedling photosynthesis and growth may be more responsive to interactions with abiotic factors, including future changes in climate, than previously estimated. The sensitivity of seedling growth to varying patterns of dynamic irradiance, and the increased likelihood of species-specific responses through interactions with environmental factors, indicates the potential for sunflecks to influence regeneration processes, and hence forest structure and composition.

Key words: Dipterocarpaceae, dynamic photosynthesis, elevated CO<sub>2</sub>, forest understorey, heat stress, photorespiration, photosynthetic induction, seedling regeneration, *Shorea leprosula*, stomatal conductance.

## Introduction

Sunflecks have been recognized as an important source of energy for tree seedlings in tropical rain forests for many decades. Following early work by Evans (1939, 1956), the responses of a diversity of species have been examined in response to flecked light, under both natural and controlled environment conditions, in order to address questions at a range of scales from the biochemical to the ecological. The majority of these studies have focused on three key issues: (i) the physical nature of sunflecks (activity, pattern, light quality) in diverse canopy structures; (ii) the limitations to CO<sub>2</sub> fixation imposed by sunflecks and quantification of the resulting carbon gain; and (iii) the differences between species in their responses to sunflecks; all of which have been thoroughly reviewed (see, for example, Chazdon, 1988; Pearcy, 1990; Chazdon and Pearcy, 1991; Baldocchi and Collineau, 1994; Pearcy *et al.*, 1994; Chazdon *et al.*, 1996). However, the understanding of plant responses to sunflecks has lagged behind in three important areas. First, most studies regard sunflecks as a resource of light energy, but do not consider the potential for stress during sunflecks from excess photosynthetic photon flux density (PPFD), temperature or leaf to air vapour pressure deficit (VPD). Second, little is known about how environmental variables, independent of sunfleck activity (e.g. elevated [CO<sub>2</sub>]), affect the use of sunflecks for photosynthetic carbon gain and growth. Third, understanding the extent to which sunflecks significantly affect seedling growth rates or survival, independent of changes in total PPFD, thereby potentially

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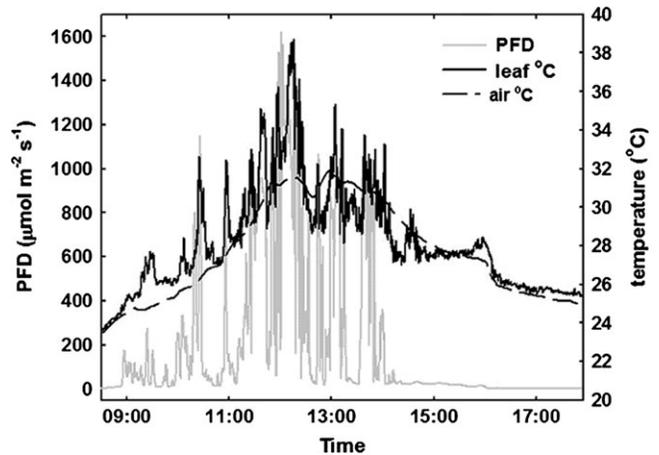
influencing interspecific competition and regeneration ecology. This synthesis discusses the results of experiments that address these issues using dipterocarp seedlings and in doing so provide further evidence for the physiological and ecological significance of sunflecks.

### Increased leaf temperature and inhibition of photosynthesis during sunflecks

It is well understood how the utilization of dynamic irradiance for photosynthetic carbon gain is limited by the duration, frequency and PPFD of sunflecks interacting with photosynthetic induction gain and loss, photosynthetic capacity and post-irradiance metabolism (reviewed in Pearcy *et al.*, 1994). However, in addition to higher PPFD, the result of the direct solar radiation incident on a leaf during a sunfleck includes increased temperature and, therefore, VPD (Young and Smith, 1979, 1983; Robichaux and Pearcy, 1980; Chazdon, 1988; Watling, 1991). Low stomatal conductance and high relative humidity should predispose tropical understorey plants to higher temperatures because they will reduce latent heat loss by transpiration. Little is known about how these potentially stressful conditions may constrain carbon gain during sunflecks (Chazdon, 1988). Assessing the ecological and physiological significance of sunflecks for seedlings requires a holistic approach that considers the trade-off between sunflecks as a resource fuelling photosynthesis, versus a set of abiotic stresses.

Tropical understorey species can mitigate against photo-damage during high PPFD sunflecks by dissipating excess excitation energy by non-photochemical quenching (Logan *et al.*, 1997; Schiefthaler *et al.*, 1999). Nonetheless, sunflecks have been observed to cause persistent photoinhibition in Australian understorey plants (Watling *et al.*, 1997b) and to reduce photosynthetic carbon gain in *Elatostema repens* grown under low light (Le Gouallec *et al.*, 1990). Inhibition of photosynthesis by excess PPFD is exacerbated if the plant is experiencing additional environmental stresses (Ludlow, 1987). Therefore, if temperatures can rise sufficiently to limit photosynthesis during sunflecks, an interaction with high VPD and excess PPFD is likely to result, magnifying the constraint upon carbon gain. Maximum leaf temperatures of 30 °C in the Hawaiian understorey were above the temperature optimum for photosynthesis in *Euphorbia forbesii* and *Claoxylon sandwicense* and, therefore, could have directly constrained carbon gain during sunflecks (Robichaux and Pearcy, 1980).

A study of leaf temperatures of *Shorea leprosula* seedlings in the dipterocarp rain forest of SE Asia revealed that seedlings experienced temperatures up to 38 °C, with leaf temperature tracking sunfleck activity (Leakey *et al.*, 2003b) (Fig. 1). Consequently, up to 56% of total daily PPFD was received at temperatures above 30 °C. To investigate the physiological significance of these high temperatures during sunflecks, the inhibition of photosynthesis at 38 °C relative

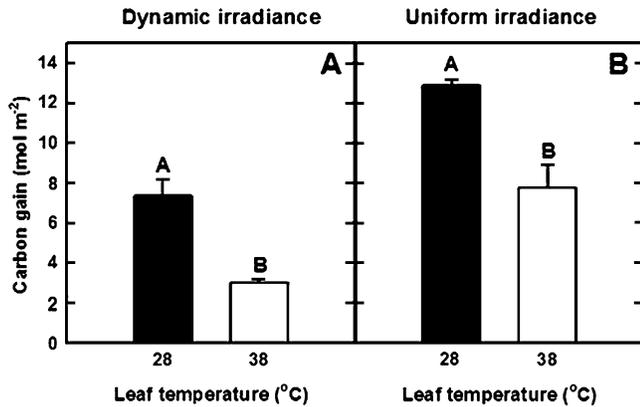


**Fig. 1.** Representative traces over the diurnal period of: leaf temperature (black line) of a *S. leprosula* seedling in a tropical rainforest understorey, PPFD incident on the leaf (grey line) and air temperature (dashed line). (Redrawn from Leakey *et al.*, 2003b.)

to 28 °C was compared under uniform PPFD, versus a simulated sequence of sunflecks, in controlled environment conditions (Leakey *et al.*, 2003b). Saturating PPFD in both uniform and dynamic irradiance treatments was 539  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , while leaf-to-air VPD was maintained at or below 1.3 kPa throughout gas exchange measurements. These conditions allowed photosynthetic responses to temperature to be assessed independently from the potentially photo-inhibitory effects of excess PPFD and low VPD.

The light-saturated rate of photosynthesis ( $A_{\text{max}}$ ) in *S. leprosula* under uniform irradiance was optimal at 29 °C, and progressively inhibited with increased temperature. Consequently,  $A_{\text{max}}$  was 40% lower at 38 °C compared with 28 °C. Inversely, calculated rates of photorespiration ( $R_p$ ) increased significantly with rising temperatures above 30 °C. This is consistent with previous reports of photosynthetic and photorespiratory responses to high temperatures and is most likely due to unfavourable changes in the differential solubility of  $\text{CO}_2$  and  $\text{O}_2$  (Ku and Edwards, 1977; Monson *et al.*, 1982) and the kinetic properties of Rubisco (Monson *et al.*, 1982; Jordan and Ogren, 1984; Sage and Sharkey, 1987). It has also been suggested that reduction in the activation state of Rubisco may play a role (mediated by Rubisco activase activity; Law and Crafts-Brandner, 1999; Crafts-Brandner and Salvucci, 2000).

To assess dynamic photosynthesis, leaves were exposed to a PPFD of 30  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , until steady-state gas exchange was achieved. They were then subjected to ten, 3 min flecks of 539  $\mu\text{mol m}^{-2} \text{s}^{-1}$  separated by 1 min low light periods of 30  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Inhibition of carbon gain at 38 °C compared with 28 °C during this dynamic irradiance was greater (−59%; Fig. 2A) than for the same duration of uniform irradiance (−40%, Fig. 2B). The additional inhibition of carbon gain by high temperatures during sunflecks was due to reductions in lightfleck utilization efficiency (LUE) (Fig. 3A).



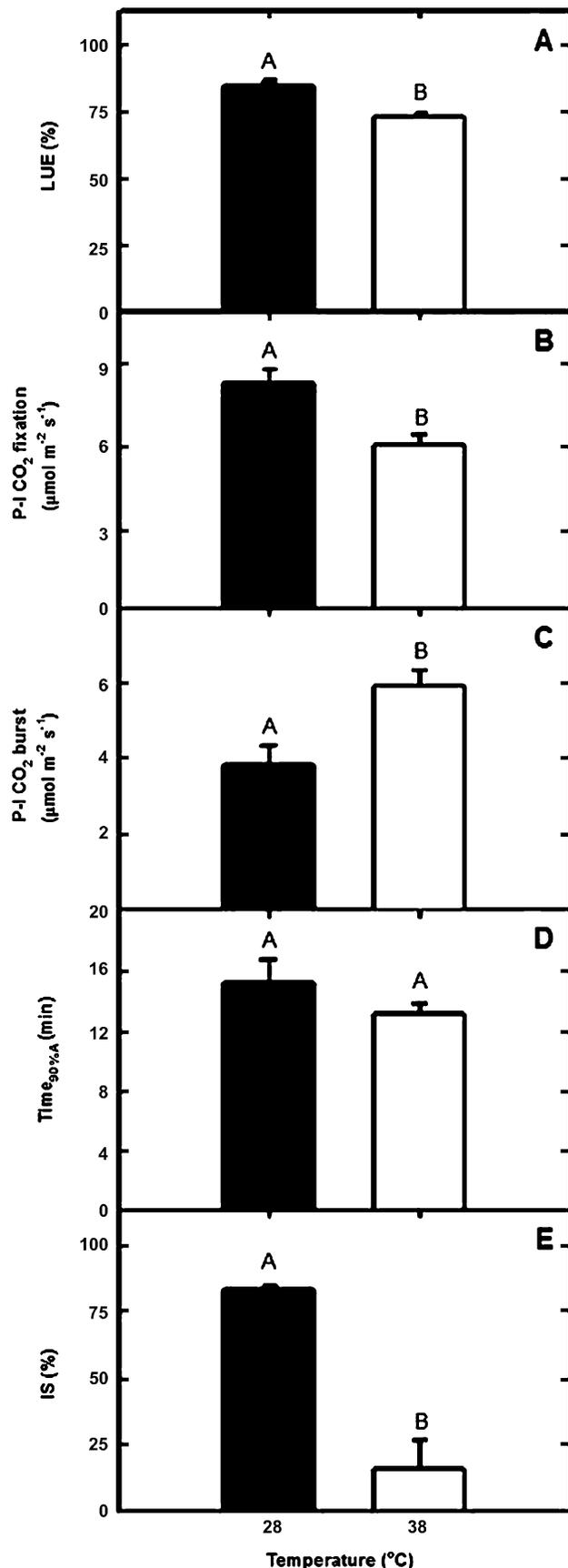
**Fig. 2.** Carbon gain of youngest fully expanded leaf of *S. leprosula* seedlings during 40 min irradiance treatment of (A) sequence of simulated sunflecks and (B) saturating uniform irradiance, at 28 °C and 38 °C. Carbon gain under uniform irradiance was calculated by integrating instantaneous photosynthetic rates, at 28 °C and 38 °C on temperature response curves, over the treatment period. Values are means ( $\pm$ SE),  $n=5$ . Bars not sharing a common letter differ significantly ( $t$ -test,  $P < 0.05$ ). (Modified from Leakey *et al.*, 2003b.)

Reduced post-irradiance  $\text{CO}_2$  fixation (Fig. 3B) and greater post-irradiance  $\text{CO}_2$  burst (Fig. 3C) both contributed to the decrease in LUE. Photosynthetic and photorespiratory flux drives post-irradiance  $\text{CO}_2$  fixation and post-irradiance  $\text{CO}_2$  burst, respectively (Sharkey *et al.*, 1986; Rawsthorne and Hylton, 1991). Inhibition of steady-state photosynthesis, alongside greater  $R_p$  at 38 °C, compared with 28 °C, could have driven the response. Short-term treatments of low  $\text{CO}_2$  concentration ( $[\text{CO}_2]$ ), high  $\text{O}_2$  and high temperatures have previously produced equivalent results (Doehrlert *et al.*, 1979; Peterson, 1983; Vines *et al.*, 1983; Laisk *et al.*, 1984). The alteration of post-irradiance metabolism at high temperatures could be greater under natural irradiance patterns of short, high frequency flecks where post-irradiance carbon gain is a larger fraction of photosynthetic carbon gain (Percy, 1990).

Meanwhile, there was no significant change in the rate of photosynthetic induction gain, measured as  $\text{Time}_{90\%A}$  (Fig. 3D). This result is consistent with increased photorespiration causing the high temperature inhibition of photosynthesis, but not with Rubisco activase deactivation playing a role in the effect. Faster photosynthetic induction loss during shade periods between flecks was also implicated in reducing LUE at 38 °C. This was indicated by a large reduction, at 38 °C, in the induction state remaining 10 min after a transition from light to dark (Fig. 3E). This was, at least partially, caused by accelerated stomatal closure at 38 °C. However, increased deactivation of enzymes responsible for RuBP regeneration or Rubisco may also have occurred in the shade at higher temperatures (Sassenrath-Cole and Percy, 1992; Ernstsens *et al.*, 1997). In natural irradiance regimes, where many shade periods may be of this duration ( $\leq 10$  min; Percy *et al.*, 1994; Leakey, 2002), this could significantly decrease photosynthetic carbon gain during subsequent flecks.

Clearly, leaves of *S. leprosula* experience high temperatures, notably in conjunction with periods of high PPFD thought to drive photosynthetic carbon gain. In addition, dynamic photosynthesis is more sensitive to inhibition by super-optimal temperatures than steady-state photosynthesis. Thus, perhaps the current dogma that sunfleck activity is directly associated with greater carbon gain is misleading. Further experiments are needed to determine whether the transient increases in leaf temperature observed in the field have the same inhibitory effects. Nonetheless, high temperatures may play an important role in constraining the potential benefits of long sunflecks, or even short sunflecks at high frequency. This experiment was designed to avoid severe photoinhibition due to interactions between high temperature, low VPD, and excess PPFD during sunflecks. Yet, in the field, these three conditions are unavoidably simultaneous. They interact to cause photoinhibition and photodamage under uniform irradiance treatments (Kitao *et al.*, 2000). Therefore, dynamic photosynthesis might also be inhibited to such an extent that excess excitation energy from light harvesting could exceed the capacity for energy dissipation and photoprotection, causing photodamage. It appears that high temperature inhibition of photosynthesis during sunflecks could have significant effects upon seedling carbon balance and, therefore, probably also on growth and survival (Chazdon, 1988; Fetcher *et al.*, 1994; Press *et al.*, 1996). High temperatures can also inhibit photosynthesis under dynamic irradiance regimes in the canopy (Roden and Percy, 1993; Singaas and Sharkey, 1998). A number of species rapidly release isoprene from their leaves in response to short-term increases in leaf temperature (Sharkey and Yeh, 2001). Emission of isoprene confers resistance to heat stress under these conditions (Sharkey and Yeh, 2001). The evolution of this stress tolerance mechanism, which causes significant loss of carbon from the leaf, suggests that dynamic heat stress may be of considerable adaptive significance.

Field measurements are required to determine the frequency and extent to which the potential of sunflecks to facilitate carbon gain is met. This will be difficult because the standard procedure of using gas exchange to measure carbon gain is constrained by the use of leaf chambers, which buffer any external changes in temperature and VPD. This may explain why the effects of temperature during sunflecks have not been addressed further, and also suggests that some previous measurements of daily carbon gain may have been overestimates. Further studies are also needed to consider the effects of (i) potential acclimation to dynamic temperatures during sunflecks, and (ii) the variation in temperature responses between different patterns of sunflecks, before realistic predictions of field responses can be made from experimental data. This will be particularly important as global climate change increases maximum temperatures and the number of hot days (Houghton *et al.*, 2001).



### Interaction of dynamic photosynthesis with independent environmental factors

The interaction between photosynthesis and the environment is one of the central themes of plant ecophysiological research. Many studies have investigated the relationships between photosynthesis and atmospheric, edaphic or biotic variables, along with their implications for ecological processes, crop productivity, feedbacks to climate, and processes of natural selection (Larcher, 1995; Baker and Bowyer, 1994; Press *et al.*, 1999). However, the great majority of this large body of work has considered photosynthesis as a process operating under steady-state conditions of uniform irradiance. In stark contrast, photosynthesis is driven by highly dynamic irradiance regimes in many vegetation types, from forests to herbaceous crop canopies (Chazdon, 1988; Tang *et al.*, 1988; Pearcy *et al.*, 1990, 1994). If the impacts of environmental variables on photosynthesis under sunflecks differ significantly from those under uniform irradiance, then it indicates a potentially important source of error in the present interpretation of plant–environment interactions under field conditions for either dipterocarp seedlings, or other species growing under dynamic irradiance regimes.

Global climate change is likely to lead to elevated atmospheric [CO<sub>2</sub>] and ozone concentrations, higher maximum temperatures, and more hot days over land areas, as well as an increased frequency of drought events (Houghton *et al.*, 2001; US National Research Council, 2002). The responses of forests will be strongly influenced by the effect of elevated [CO<sub>2</sub>] upon dynamic photosynthesis because the light environment is highly heterogeneous (Pearcy, 1987; Chazdon, 1988). Thus, the photosynthesis and growth of *S. leprosula* seedlings were assessed over 216 d under controlled environment conditions of ambient (376 µmol mol<sup>-1</sup>) or elevated [CO<sub>2</sub>] (710 µmol mol<sup>-1</sup>). Seedlings were supplied with either uniform or flecked irradiance. Total daily PPFD in each treatment was equal (7.7 mol m<sup>-2</sup> d<sup>-1</sup>), and typical of an understory site with a patchy canopy (ADB Leakey, unpublished data). In the continuous light treatment the PPFD at plant height was ~170 µmol m<sup>-2</sup> s<sup>-1</sup>. The dynamic irradiance treatment of repeated clusters of flecks separated by continuous low background PPFD was a simplified simulation of field conditions (Pearcy, 1987; Chazdon, 1988; ADB Leakey, unpublished data). During each photoperiod, plants received six clusters of flecks. Each cluster consisted of 12, 3 min flecks of

**Fig. 3.** (A) Light utilization efficiency (LUE) (B) post-irradiance (P-I) CO<sub>2</sub> fixation, (C) post-irradiance (P-I) CO<sub>2</sub> burst, and (D) time for 90% completion of photosynthetic induction (Time<sub>90%A</sub>), of *S. leprosula* during a simulated sequence of sunflecks, at 28 °C or 38 °C. (E) Induction state after 10 min shade (IS%) as a percentage of values at saturating irradiance of *S. leprosula*, at 28 °C or 38 °C. Values are means (±SE), *n*=5. Bars not sharing a common letter differ significantly (*t*-test, *P* < 0.05). (Modified from Leakey, 2002; Leakey *et al.*, 2003b)

$\sim 525 \mu\text{mol m}^{-2} \text{s}^{-1}$ , separated by 1 min shade periods of  $\sim 30 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Between successive clusters there was a 78 min shade period of  $\sim 30 \mu\text{mol m}^{-2} \text{s}^{-1}$ , which allowed photosynthetic induction to relax fully before the next fleck cluster.

The relative stimulation of biomass accumulation (Fig. 4A) and photosynthetic carbon gain (Fig. 4B) in *S. leprosula* by elevated  $[\text{CO}_2]$  concentrations was significantly greater under sunflecks, compared with uniform irradiance. Greater photosynthetic carbon gain from flecked irradiance resulted from the same improvement in photosynthetic capacity under saturating and shade PPFD as in the uniform irradiance treatment, but the effect was amplified by enhanced LUE. Greater LUE at elevated  $[\text{CO}_2]$  was the combined result of faster photosynthetic induction gain, slower photosynthetic induction loss (after 5 min shade), greater post-irradiance  $\text{CO}_2$  fixation, and lower post-irradiance  $\text{CO}_2$  burst (Figs 5, 6).

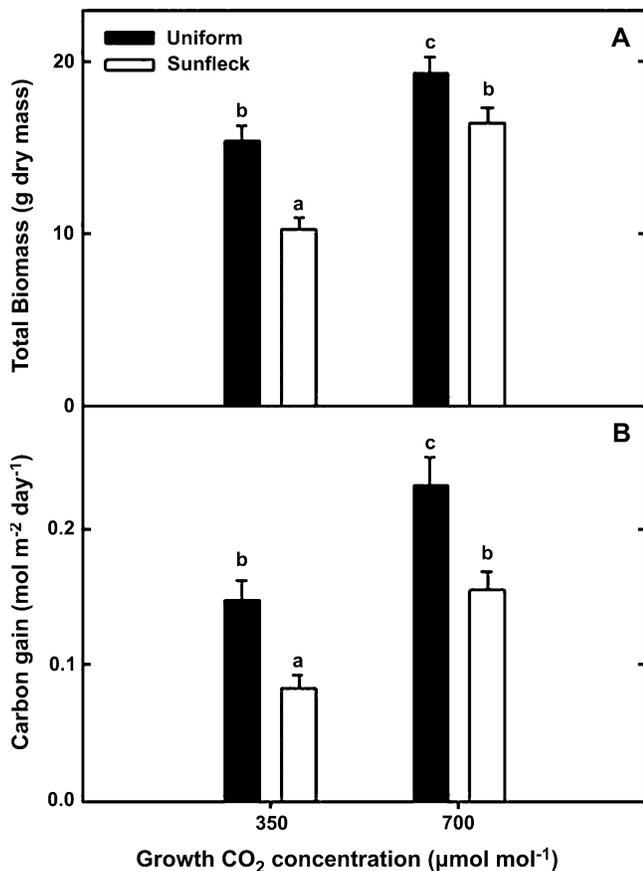
The accelerated photosynthetic induction at elevated  $[\text{CO}_2]$  was probably facilitated by a reduced requirement for stomatal opening in order for intercellular  $[\text{CO}_2]$  to reach

the operating point for saturating irradiance. Lower stomatal conductance and faster photosynthetic induction at elevated  $[\text{CO}_2]$  have also been observed in a  $\text{C}_4$  grass (Knapp *et al.*, 1994). By contrast, stomatal effects did not appear to be involved in the slower loss of photosynthetic induction state at elevated  $[\text{CO}_2]$  after a light-to-shade transition. Instead, it might result from slower deactivation in the shade of the enzymes responsible for RuBP regeneration or Rubisco (Sassenrath-Cole and Pearcy, 1992; Ernstsens *et al.*, 1997; Naumburg and Ellsworth, 2000).

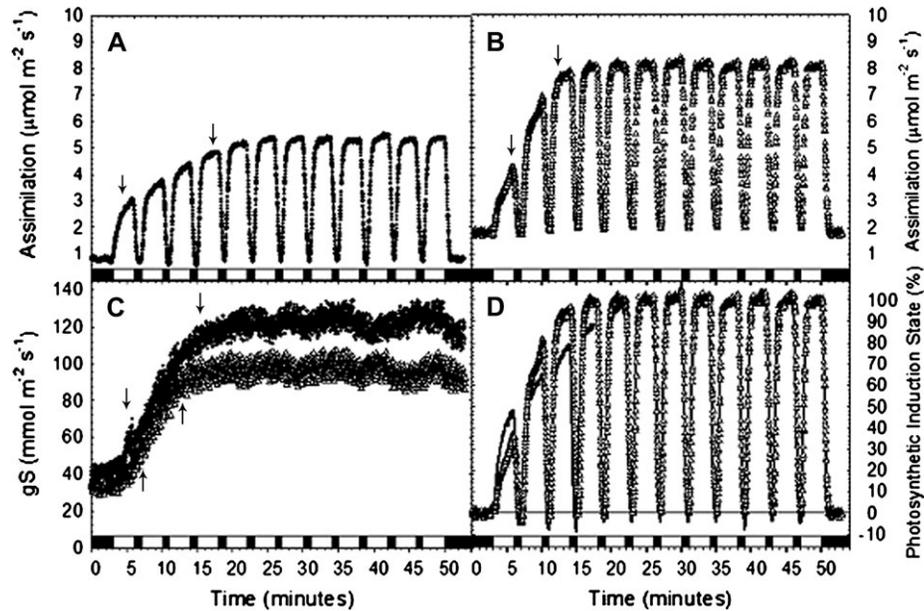
Photosynthesis was greater at elevated  $[\text{CO}_2]$ , the cause of which has been established as greater  $\text{CO}_2$  saturation of Rubisco and reduced photorespiration (Stitt, 1991). Post-irradiance metabolism is associated with metabolism of intermediates in the photosynthetic and photorespiratory pathways, respectively (Sharkey *et al.*, 1986; Rawsthorne and Hylton, 1991). The increased post-irradiance  $\text{CO}_2$  fixation (+14%) and reduced post-irradiance  $\text{CO}_2$  burst (−88%) in seedlings growing at elevated  $[\text{CO}_2]$ , therefore, followed predictions on the response of photosynthetic and photorespiratory flux to elevated  $[\text{CO}_2]$ , as it did in the earlier experiment at high temperature. Short-term treatments of high  $[\text{CO}_2]$  or low  $\text{O}_2$  have also generated such effects previously (Doehlert *et al.*, 1979; Peterson, 1983; Vines *et al.*, 1983; Laisk *et al.*, 1984).

The stimulation of LUE at elevated  $[\text{CO}_2]$  appears to be primarily attributable to reduced stomatal conductance and photorespiration. These are direct responses to elevated  $[\text{CO}_2]$  which are not subject to acclimation over time (Long *et al.*, 2004). Consequently, the enhancement of LUE, and increased sensitivity of carbon gain to elevated  $[\text{CO}_2]$  under sunflecks, may be found across a range of natural dynamic irradiance regimes, species, and environmental conditions. Patterns of short, high frequency flecks, where post-irradiance metabolism contributes a greater proportion of net carbon gain, are common in understory environments (Percy, 1990). An increase in post-irradiance carbon gain at elevated  $[\text{CO}_2]$  would therefore be expected. In addition, shade periods of 5 min duration are also frequent in natural irradiance regimes (Percy, 1994; Leakey *et al.*, 2003a). The rate of photosynthetic induction loss across this period was lower at elevated  $[\text{CO}_2]$ . This would further stimulate photosynthetic carbon gain during subsequent flecks at elevated  $[\text{CO}_2]$ .

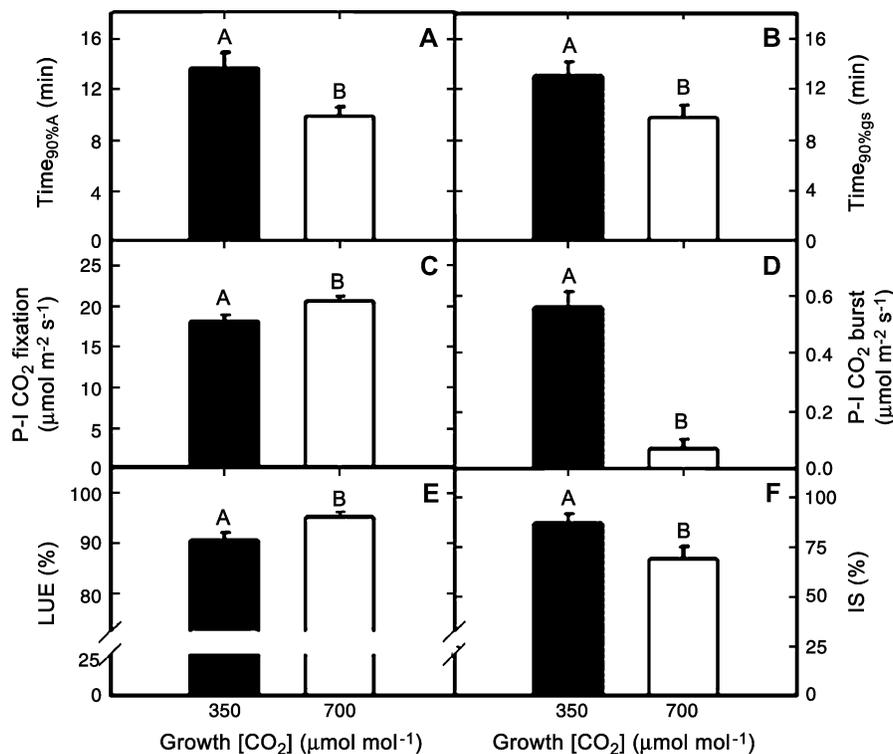
There is also evidence for enhancement of photosynthetic carbon gain during sunflecks by elevated  $[\text{CO}_2]$  ( $550 \mu\text{mol mol}^{-1}$ ) in temperate forest tree seedlings, due to greater light-saturated rates of photosynthesis and maximum electron transport capacity (DeLucia and Thomas, 2000) and slower photosynthetic induction loss (Naumburg and Ellsworth, 2000). A modelling exercise parameterized using the measurements of Naumburg and Ellsworth (2000) indicated that the greater relative enhancement of carbon gain at elevated  $[\text{CO}_2]$  ( $550 \mu\text{mol mol}^{-1}$ ) under dynamic irradiance, compared with uniform irradiance, was greatest



**Fig. 4.** (A) Calculated rates of daily photosynthetic carbon gain, and (B) total plant biomass after 216 d growth at either ambient or elevated  $\text{CO}_2$  with uniform or flecked irradiance, of *S. leprosula*. Values are means ( $\pm$ SE),  $n=6$ . Bars not sharing a common letter differ significantly (Tukey multiple comparison test  $P < 0.05$ ). (Modified from Leakey *et al.*, 2002.)



**Fig. 5.** Representative time-courses of net photosynthetic rates (A, B), stomatal conductance (gS) (C), and photosynthetic induction state (D) of *S. leprosula* grown and measured in ambient (closed circles) and elevated (open triangles)  $[\text{CO}_2]$ , during a simulated sequence of sunflecks. Flecks are of 3 min duration (white bands) separated by 1 min shade periods (dark bands). Arrows indicate time for induction to 50% or 90% of parameter maximum. (Redrawn from Leakey *et al.*, 2002.)



**Fig. 6.** (A) Time for 90% completion of photosynthetic induction ( $\text{Time}_{90\%A}$ ), (B) time for 90% completion of stomatal opening ( $\text{Time}_{90\%gs}$ ), (C) post-irradiance  $\text{CO}_2$  fixation, (D) post-irradiance  $\text{CO}_2$  burst, and (E) light utilization efficiency (LUE) of *S. leprosula*, measured and grown at either ambient or elevated  $[\text{CO}_2]$ , in response to a sequence of sunflecks simulating the growth irradiance regime. (F) Induction state after 5 min shade (IS%) as a percentage of values at saturating irradiance of *S. leprosula* measured and grown at either ambient or elevated  $[\text{CO}_2]$ . Values are means ( $\pm$ SE),  $n=6$ . Bars not sharing a common letter differ significantly ( $t$ -test,  $P < 0.05$ ). (Modified from Leakey *et al.*, 2002.)

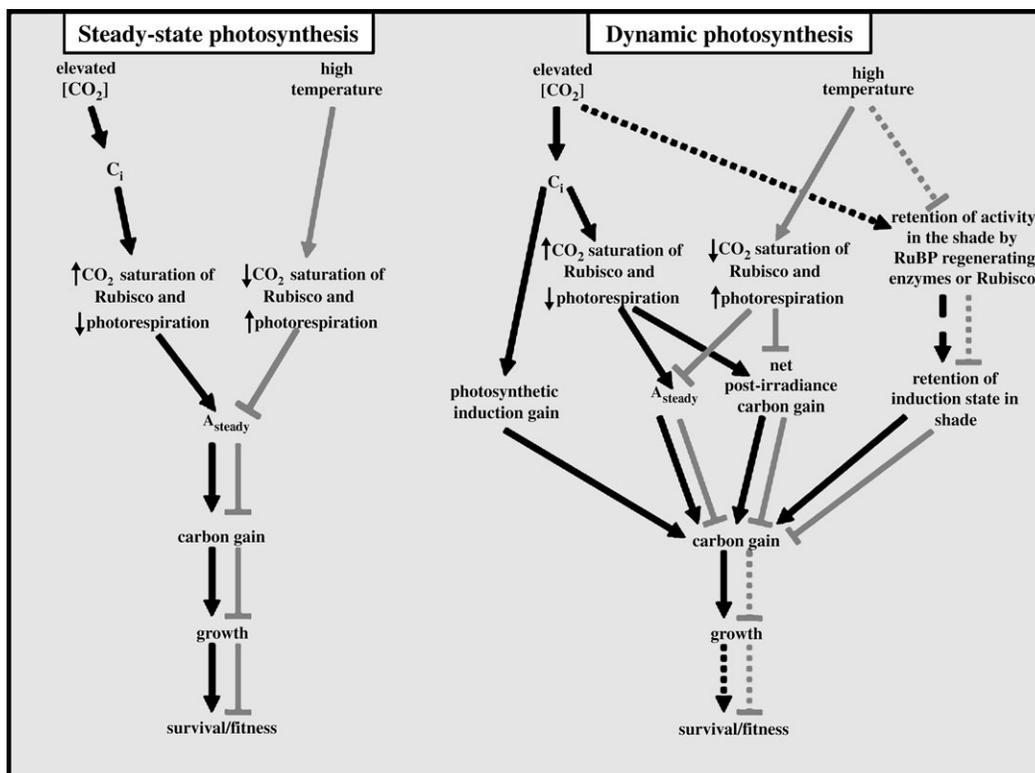
at sites receiving low total irradiance (<3% of above-canopy PPF; Naumburg *et al.*, 2001). The interaction effect was not significant at sites receiving higher total irradiance (10–20% of above-canopy PPF), where the limitations to photosynthesis imposed by stomatal conductance and photosynthetic induction were lower.

Greater stimulation of carbon gain by elevated  $\text{CO}_2$  under flecked irradiance obviously has important implications for predicting global climate change effects on forests. Elevated  $[\text{CO}_2]$  may allow greater seedling growth and survivorship in the understorey in the future. It may have an impact already, since  $[\text{CO}_2]$  at seedling height above the forest floor can be significantly elevated in the morning hours by residual  $\text{CO}_2$  from night-time respiration, particularly in closed forest sites with little air movement (Buchmann *et al.*, 1997; Holtum and Winter, 2001; Leakey, 2002).

The direct effects of elevated  $[\text{CO}_2]$  and high temperature on steady-state photosynthesis are mediated by alteration of the  $\text{CO}_2$  saturation and reaction kinetics of the Rubisco enzyme (Fig. 7), with consequences for carbon gain and plant growth across all plant growth forms and biomes (Berry and Björkman, 1980; Long *et al.*, 2004). In rare experiments, the true ecological significance of these abiotic factors has also been quantified as impacts upon plant survival and fitness (for example, fecundity; LaDeau and Clark, 2001). The

experiments synthesized here have indicated greater sensitivity of photosynthesis to elevated  $[\text{CO}_2]$  and high temperature under dynamic irradiance compared with uniform irradiance. This results from the greater complexity of the mechanisms limiting carbon gain (Fig. 7). Compounding modification of steady-state photosynthetic capacity ( $A_{\text{steady}}$ ), are changes in LUE. This adjusts via alterations in: (i) photosynthetic induction gain; (ii) net post-irradiance carbon gain; and (iii) retention of induction state in the shade. These initial experiments suggest that elevated  $[\text{CO}_2]$  impacts all of these components, while high temperatures reduce only net post-irradiance carbon gain and retention of induction state in the shade. The interaction between elevated  $[\text{CO}_2]$  and increasing temperature is very important in the context of climate change. As temperature rises the relative stimulation of photosynthesis by elevated  $[\text{CO}_2]$  increases (Long, 1991). Given the overlap in the mechanisms by which elevated  $[\text{CO}_2]$  and high temperature affect dynamic photosynthesis (Fig. 7), this interaction may be even more important under dynamic irradiance regimes.

While elevated  $[\text{CO}_2]$  and high temperature effects on photosynthesis have been demonstrated to alter plant survival and fitness, correlations between the commonly measured and modelled parameters of light-saturated photosynthesis, productivity and yield are weak (Gifford and



**Fig. 7.** A simplified diagram comparing the mechanisms by which elevated  $[\text{CO}_2]$  (black) and high temperature (grey) impact photosynthesis under steady-state or dynamic irradiance regimes. Arrows indicate positive effects, barred lines indicate negative effects. Dashed lines indicate mechanism is hypothesized.  $A_{\text{steady}}$  = Steady-state photosynthetic capacity.

Evans, 1981). Predictions of the responses of net [CO<sub>2</sub>] exchange and productivity to environmental conditions will probably be improved by considering photosynthesis as a dynamic process and accounting for the greater sensitivity to elevated [CO<sub>2</sub>] and temperature that this entails. To do so will require significant advances in the modelling of dynamic photosynthesis. Semi-mechanistic models of dynamic photosynthesis (Gross *et al.*, 1991; Pearcy *et al.*, 1997; Kirschbaum *et al.*, 1998) have been applied to evaluating the carbon gain of middle- and understorey leaves under well-quantified sunfleck regimes (Tang *et al.*, 1988; Pearcy *et al.*, 1990; Baldocchi and Collineau, 1994; Vierling and Wessman, 2000). However, these models do not make any representation of post-irradiance metabolism. In addition, a lack of knowledge has prevented any mechanistic simulation of stomatal conductance or induction state. However, the recent publication of new stomatal (Buckley *et al.*, 2003) and photosynthetic models (Zhu, 2004), with an increasing emphasis on mechanism and the capability to reproduce dynamic responses, is cause for optimism. Models provide the only realistic method by which the impact of abiotic factors on dynamic photosynthesis may be tested across the huge range of total PPFD and sunfleck patterns which are found in plant canopies. The use of reverse-ray tracing algorithms to simulate the light environment of leaves at different positions and orientations in a canopy will be particularly useful in this respect (Zhu *et al.*, 2004).

The significantly greater impact of elevated [CO<sub>2</sub>] and high temperatures on carbon gain during sunflecks, compared with uniform irradiance, makes sunflecks more physiologically and ecologically significant than previously recognized. It is also possible that dynamic photosynthesis, and therefore carbon gain under field conditions, may be more sensitive to other stresses such as elevated ozone and drought, than previously accounted for. In addition, as dynamic gas exchange is considered more broadly, efforts are needed to evolve from the current carbon-centric perspective and expand upon the studies which report the physiological and ecological significance of sunflecks to plant water relations (Woodward, 1981; Knapp and Smith, 1987; Barradas *et al.*, 1994).

### Sunflecks are a heterogeneous resource affecting seedling photosynthesis and growth

The growth and survival of tree seedlings in tropical rain forests are primarily limited by their ability to maintain a positive carbon balance. This is determined by rates of photosynthesis under the light-limited conditions and carbon loss resulting from respiration, herbivory, pathogens, and physical damage (Chazdon, 1988; Fetcher *et al.*, 1994; Kitajima, 1996; Press *et al.*, 1996). Sunflecks contribute 10–90% of the total daily PPFD received by understorey plants, with this fraction being highly spatially variable, even on a small scale (Pearcy, 1983; Chazdon, 1986). The activity of sun-

flecks is also highly variable within the diurnal period (Evans, 1956; Ashton, 1958; Chazdon, 1988) and over days or weeks, depending on canopy structure and weather conditions (Chazdon, 1988).

Evidence for sunflecks having an ecologically significant role in determining seedling growth is based on: (i) field data of correlations between sunfleck activity (the fraction of total daily PPFD incident as sunflecks or the total min of sunflecks per day) and daily carbon gain or relative growth rates (Pearcy, 1983; Oberbauer *et al.*, 1988; Pfitsch and Pearcy, 1989; Washitani and Tang, 1991); (ii) controlled environment studies in which tropical species, growing under equal total daily PPFD, displayed significantly different growth rates under different sunfleck patterns or sunflecks versus uniform irradiance (Sims and Pearcy, 1993; Watling *et al.*, 1997a); and (iii) photosynthetic responses to controlled sequences of lightflecks differing in duration, intensity, and frequency suggest that carbon gain would be affected significantly by variation in sunfleck patterns of the magnitude observed (Pearcy *et al.*, 1994). However, the evidence from correlations between sunfleck activity and seedling carbon gain or growth rates could be misleading because sunfleck activity was also correlated with total daily PPFD, which could account for the variation in growth rates observed (Chazdon, 1988). Meanwhile, the data from controlled environment studies demonstrate the mechanisms by which sunflecks may influence seedling growth, but are highly simplified simulations of field conditions. Validation of the findings is required from experiments conducted on seedlings in the forest understorey.

Within the understorey of the primary, lowland dipterocarp forest at Danum Valley (Sabah, East Malaysia) there was significant heterogeneity in sunfleck activity and patterns of sunflecks across a range of temporal and spatial scales (Leakey, 2002). For instance, analysis of irradiance regimes at 16 understorey sites, not differing significantly in the mean total daily PPFD received, indicated significant variation in: (i) the fraction of total daily PPFD incident as sunflecks; (ii) the duration of sunflecks, and, (iii) the mean PPFD of sunflecks. Therefore, dipterocarp seedlings existed under conditions with the potential for patterns of sunflecks to affect seedling growth rates.

To test this issue, the photosynthetic and growth performance of two species of dipterocarp seedlings were assessed under two dynamic irradiance regimes, characterized by either long sunflecks (LF) or short sunflecks (SF) (Leakey *et al.*, 2003a). There was no significant difference in the mean total daily PPFD received by the seedlings in the two treatments ( $\sim 3.3 \text{ mol m}^{-2} \text{ d}^{-1}$ ). Sunflecks were defined as periods of direct PPFD separated by diffuse PPFD. Under LF, sunflecks contributed 45% of total daily PPFD and were received over 11.7% of the photoperiod. By contrast, under SF, sunflecks contributed a significantly greater fraction of total daily PPFD (61%), but over a smaller fraction of the day (6.1%). The pattern of sunflecks under LF and SF

differed in duration and intensity. In the SF treatment, more than 50% of sunflecks were 10 min or less in duration and all were less than 60 min long (Fig. 8A). In the LF treatment, only 25% had durations shorter than 10 min, while 37% were longer than 60 min. Also, the range of mean PPF of sunflecks in the LF treatment (maximum PPF=750  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) was considerably smaller compared with the SF treatment (maximum PPF=1700  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) (Fig. 8B).

Both species are climax-canopy species, but *Shorea leprosula* is relatively fast-growing and light-demanding while *Hopea nervosa* is slower growing and very shade-tolerant (Burgess, 1966; Zipperlen and Press, 1996). Relative growth rates of *S. leprosula* and *H. nervosa* were both 4-fold greater in response to long sunflecks compared with short sunflecks (Fig. 9). The magnitude of the treatment effect on growth was significantly greater than that observed for different patterns of sunflecks, or sunflecks versus uniform irradiance, under controlled environment conditions (Sims and Pearcy, 1993; Watling *et al.*, 1997a) and comparable to the differences in growth at sites varying in total daily PPF between 2.2–7.7  $\text{mol m}^{-2} \text{d}^{-1}$  (Zipperlen and Press, 1996). Seedling *RGR* was strongly, positively associated with growth rate per unit leaf area and  $A_{\text{max}}$ , suggesting that greater seedling growth under LF was primarily associated with changes in photosynthetic physi-

ology rather than allometry (see data in Leakey *et al.*, 2003a). This has also been observed in other shade-tolerant, tropical forest species in response to variation in total PPF (Popma and Bongers, 1988; Osunkoya and Ash, 1991) or patterns of sunflecks (Sims and Pearcy, 1993; Watling *et al.*, 1997a).

Greater carbon gain under the long fleck regime was associated with a significantly, greater  $A_{\text{max}}$  compared with under short flecks. Phenotypic plasticity can enhance acquisition of resources under heterogeneous conditions (Robinson, 1994; de Kroon and Hutchings, 1995), but other studies have observed plasticity at the leaf scale only in response to variation in total PPF and not the pattern in which it is incident upon plants (Nobel, 1976; Chabot *et al.*, 1979; Nobel and Hartsock, 1981; Sims and Pearcy, 1993; Watling *et al.*, 1997a; Leakey *et al.*, 2002). The impact of patterns of dynamic irradiance observed under field conditions may have been due to the longer period of experimental treatments than in the controlled environment studies cited, or the combination of environmental signals arising from differences in patterns of sunflecks in the forest. Yin and Johnson (2000) demonstrated the ability of higher plants to sense and respond specifically to different patterns of dynamic irradiance during the process of acclimation to total PPF. Heterogeneity in patterns of sunflecks has greater physiological significance and potential to affect carbon gain if it can elicit changes in photosynthetic capacity in addition to the well-recognized effects on lightfleck utilization efficiency (Percy *et al.*, 1994).

Across the full range of light availability found within tropical rain forests, seedling *RGR* and  $A_{\text{max}}$  are both primarily determined by total daily PPF (Chazdon, 1988; Fetcher *et al.*, 1994). However, across the narrow range of total daily PPF at sites in this study, there was only a very weak relationship between seedling *RGR* and total daily

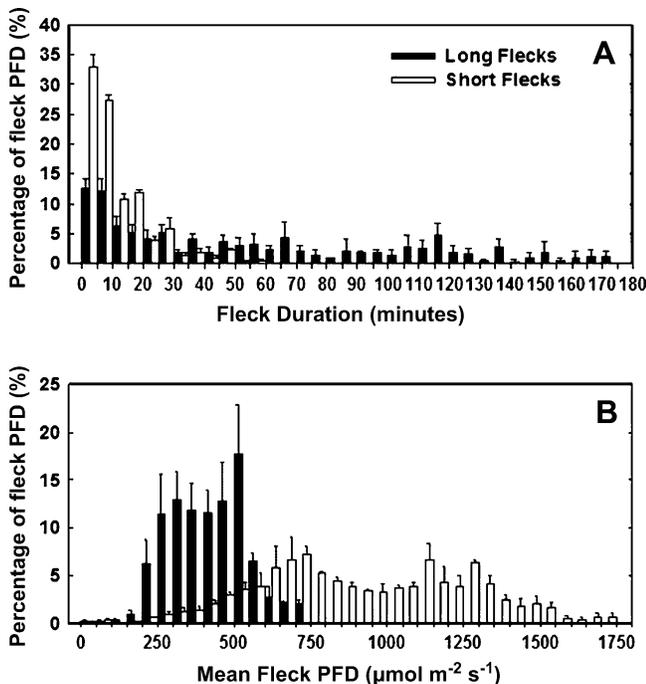


Fig. 8. Frequency histograms of (A) the fraction of total sunfleck PPF contributed by sunflecks of different durations, and (B) the fraction of total sunfleck PPF contributed by sunflecks of different mean PPF, incident upon seedlings under short fleck (filled bars) or long fleck (open bars) irradiance treatments. Values are means ( $\pm$ SE),  $n=3$ . (Modified from Leakey *et al.*, 2003a.)

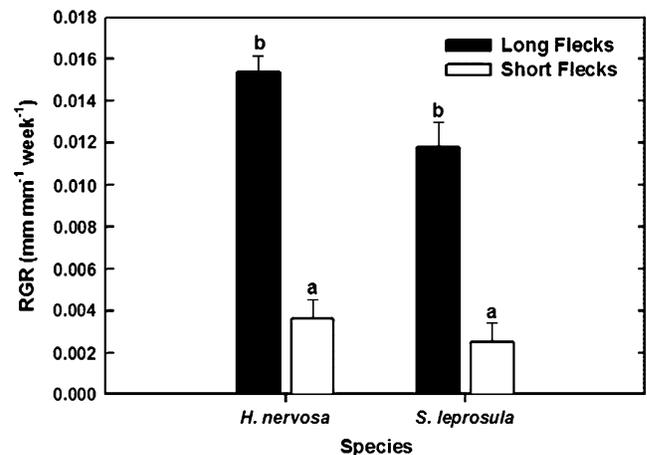


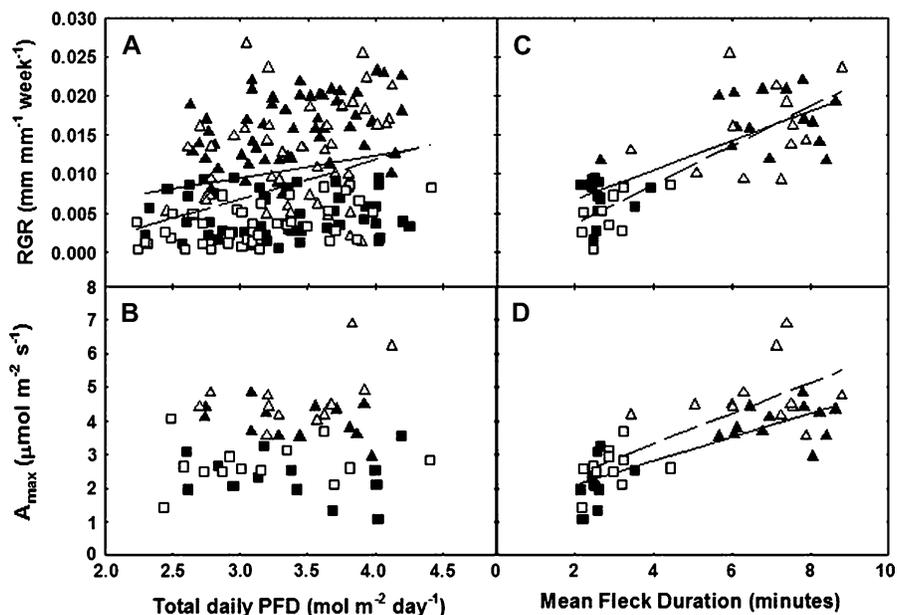
Fig. 9. Relative growth rate (*RGR*; total stem and branch length basis) of *H. nervosa* and *S. leprosula* seedlings under long fleck (filled bars) or short fleck (open bars) irradiance treatments. Values are means ( $\pm$ SE),  $n=3$ . Bars not sharing a common letter differ significantly (Tukey multiple comparison test  $P < 0.05$ ). (Redrawn from Leakey *et al.*, 2003a.)

PPFD (Fig. 10A) and variation in  $A_{\max}$  was not significantly correlated with total daily PPFD in either *S. leprosula* or *H. nervosa* (Fig. 10B). By contrast, mean fleck duration was significantly, positively correlated with both  $RGR$  and  $A_{\max}$  in *H. nervosa* and *S. leprosula* (Fig. 10C, D). This provides a mechanism to explain some of the large variation in seedling growth rates between sites in the forest understorey receiving equal total daily PPFD (Zipperlen and Press, 1996; Nicotra *et al.*, 1999; Montgomery and Chazdon, 2002). Variation in seedling growth in the understorey determines seedling size upon canopy gap creation, which is ecologically important because it is the primary determinant of seedling growth and survival in gaps in dipterocarp forest (Brown and Whitmore, 1992; Whitmore and Brown, 1996). Variation in carbon gain and growth of seedlings implies that survival is also likely to be affected by different patterns of dynamic irradiance. Seedlings can also achieve competitive success if they persist longer than competitors before canopy gap creation occurs. In both these cases, the pattern of sunflecks received by seedlings growing in the understorey could, therefore, play an important part in determining which individuals successfully out-compete neighbours and develop to maturity in the canopy.

### Potential for, and implication of, species-specific effects

Specialization of species to specific environmental conditions in the regeneration phase is the basis of the niche

differentiation theory for the maintenance of high species diversity in tropical rain forests (Watt, 1947; Grubb, 1977; Denslow, 1987; Brokaw and Busing, 2000). Along with recruitment limitation, density-dependent processes, spatial variation in the impacts of natural enemies (Janzen–Connell factors) and stochastic factors, niche differentiation governs community ecological processes (Hubbell, 2001; Wright, 2002). Variation in rates of photosynthesis between species specialized to different total daily PPFD, may contribute to niche differentiation between shade-tolerant and light-demanding guilds (Barker *et al.* 1997). However, variation in total daily PPFD alone (or gap size) is not considered to be sufficient to allow for niche differentiation between sympatric, shade-tolerant species, thus preventing competitive exclusion (Brown and Whitmore, 1992; Kennedy and Swaine, 1992; Whitmore and Brown, 1996, Barker *et al.*, 1997). However, dipterocarp species vary in their responses to total daily PPFD, excess irradiance, nutrient availability and herbivore predation (Zipperlen and Press, 1996, 1997; Scholes *et al.*, 1997; Bungard *et al.*, 2000, 2002; Liston, 2000). Given that differences between species in their responses to single variables are not sufficient to prevent competitive exclusion of sympatric species, partitioning along a combination of interacting gradients of abiotic and biotic variables is a possibility. For instance, variation between *Shorea johorensis* and *Dryobalanops lanceolata* in the ability to respond to nutrient availability differs between light environments (Bungard *et al.*, 2002). This may alter photosynthesis to favour *S. johorensis* under high sunfleck activity and nitrogen availability, but favour *D. lanceolata*



**Fig. 10.** Scatterplots of (A) relative growth rate ( $RGR$ ; total stem and branch length basis) in relation to total daily PPFD, (B) light-saturated photosynthesis ( $A_{\max}$ ) in relation to total daily PPFD, and (C) relative growth rate ( $RGR$ ; total stem and branch length basis) in relation to mean fleck duration, (D) light-saturated photosynthesis ( $A_{\max}$ ) in relation to mean fleck duration, in *H. nervosa* (closed symbols) and *S. leprosula* (open symbols) under long fleck (triangles) and short fleck (squares) irradiance treatments. Regression relationships are indicated for *H. nervosa* (solid line) and *S. leprosula* (dashed line). (Redrawn from Leakey *et al.*, 2003a.)

under low sunfleck activity and nitrogen availability. These notions are consistent with Hutchinsons's consideration of a niche as a hypervolume, in which axes of environmental conditions are utilized differentially by co-existing species (for discussion see Leibold, 1995; Bazzaz, 1996). Seedling growth has been demonstrated to respond in a species-specific manner to fine-scale variation in irradiance in the forest understorey, with species changing the rank order of their growth rates as light availability increased (Montgomery and Chazdon, 2002). It has been hypothesized that the sensitivity of seedling growth to heterogeneity in patterns of dynamic irradiance and low-light availability are mechanisms by which late-successional species performance under shaded conditions might be differentiated (Grace, 1991; Skillman *et al.*, 1999; Bungard *et al.*, 2002). Due to the intense interspecific competition that occurs at the seedling life stage and the importance of attaining height in the understorey, in order to maximize competitive advantage upon gap opening, changes in seedling growth rates may potentially play a role in determining forest composition (Lieberman *et al.*, 1995; Whitmore and Brown, 1996; Hubbell *et al.*, 1999; Schnitzer and Carson, 2001).

It is possible that species-specific photosynthetic responses to environmental conditions (including temperature and elevated [CO<sub>2</sub>]) could modify growth rates and change the outcome of interspecific interactions at the seedling lifestage (Whitmore, 1998). This likelihood increases given the greater sensitivity of carbon gain to changes in temperature and [CO<sub>2</sub>] concentrations under sunflecks than under uniform irradiance, such as are imposed in the majority of experimental studies. Given the importance of photosynthetic carbon gain to the growth of dipterocarp seedlings and the potential consequences for forest regeneration, ecosystem structure and function, the effect of changes in the environment on photosynthesis during sunflecks could have significant consequences. These include some of the areas of greatest uncertainty about global climate change, particularly secondary and tertiary effects upon forest ecosystem productivity, water use, feedbacks and feedforwards to biogeochemical cycling and biodiversity (Eamus and Jarvis, 1989; Ceulemans and Mousseau, 1994; Field *et al.*, 1995; Johnson and Ball, 1996; Drake *et al.*, 1997; Saxe *et al.*, 1998; Whitmore, 1998; Norby *et al.*, 1999).

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